B R E V I O R A

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THE STRUCTURE AND RELATIONSHIPS OF THE DROMASAURS (REPTILIA: THERAPSIDA)

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ABSTRACT. The dromasaurs are primitive anomodonts that are advanced over the venjukoviamorph grade of evolution in the reduction of the postorbital and zygomatic branches of the jugal, the reduction of the septomaxilla, and the enlargement of the area on the dentary for the insertion of the external mandibular muscle. Derived features that distinguish dromasaurs from dicynodonts are the lack of canines, the presence of a tall, slender postorbital, and the rodlike lower temporal bar. The three known dromasaurs form a structural series showing changes in the proportions of the face, a loss of premaxillary teeth, changes in the curvature of the humerus, and a loss of the ectepicondylar foramen.

INTRODUCTION

Frequently, the earliest representatives of higher taxa include groups that are at a primitive grade of evolution but are, in some features, highly specialized. Within the Therapsida, one such group is the Dromasauria. The first dromasaur to be recognized, *Galechirus,* was initially considered to be more primitive than any other therapsid known at that time (Broom, 1907). Later, two additional genera, *Galepus* and *Galeops,* were recognized, with *Galeops* being considered sufficiently distinct to be placed in its own family, the Galeopsidae (Broom, 1910, 1912). The better understanding of the dromasaur skull provided by these genera showed that they were, in many respects, derived from the primitive therapsid condition, and

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Broom (1914: 12) suggested that they were "an aberrant group of small primitive therapsids."

While there has been little question of the reality of the group, its relationships have been a matter of much uncertainty. Romer and Price (1940) noted that many of the features that separated dromasaurs from other therapsids were primitive for pelycosaurs of the suborder Edaphosauria, implying that a close relationship existed between the two groups. Later, in a review of therapsid classification, Romer and Watson (1956) suggested that a relationship between dromasaurs and dicynodonts was likely, and placed the dromasauria within the Suborder Anomodontia as an infraorder equal in rank to the Dicynodontia. The possibility that both of these relationships are correct was raised by Olson (1962), who suggested that the therapsids had a multiple origin, with the anomodonts originating from within the Edaphosauria.

Uncertainty about the relationships of the dromasaurs is a result of an incomplete understanding of the anatomy of the genera comprising the group. Although much of the skeleton is preserved, the original material consists of natural casts, so that Broom was able to determine little more than the outlines of the bones. Recognizing these problems, it was decided to reexamine the specimens studied by Broom using the methods developed for the study of specimens preserved as natural casts by Baird (1951, 1955) and Carroll (1976), in which latex peels of the specimens provide a positive image of the bones. Because it is the most completely preserved of the dromasaurs, *Galeops* will be described first.

GALEOPS

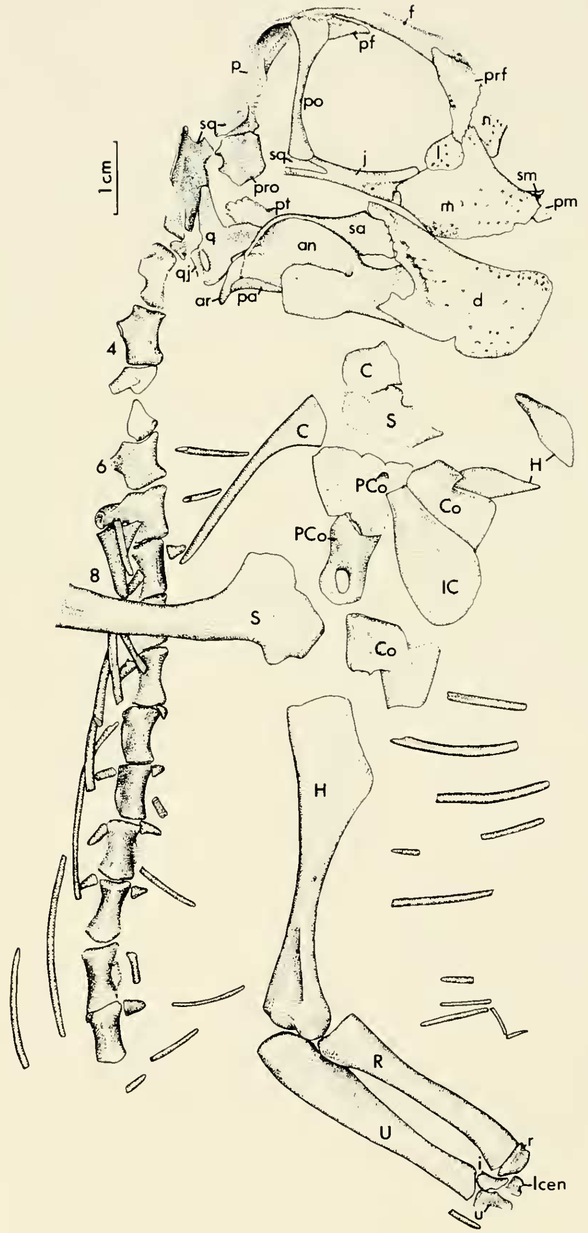
Materials and Methods: Galeops is represented by a single species, *Galeops whaitsi,* and by a single specimen, AMNH 5536, that comes from the *Tapinocephalus* zone of South Africa (Kitching, 1977). It consists of the impressions of the skull and the front half of the postcranial skeleton in a fine-grained sandstone. Both part and counterpart are present. Latex peels of the specimen provided a positive image of the skeleton, and in some cases, it was possible to cast the two halves of the individual elements and join them together to give three-dimensional replicas of the original bone.

Skull Roof: The skull of *Galeops* (Figs. 1–5) is small for a therapsid, its length from snout to quadrate being 55 mm. The orbits and external narial openings are large and face laterally. The face and postorbital regions are short. Sclerotic rings are present. The ventral margin of the postorbital region is deeply emarginated, reducing the zygomatic bar to a slender rod. The posterior edge of the upper temporal opening is folded backwards, providing a large area for the temporal muscles. No such outfolding of the squamosal is present ventral to the zygomatic bar. The occiput slopes forward and grades into the skull roof. A large pineal opening is present at the level of the frontal-parietal suture (Fig. 4). The teeth are reduced in size and are restricted to the maxilla—presumably a horny beak would have been present anteriorly.

Much of the lateral surface of the face is formed by the maxilla. In lateral view, this bone is triangular with its apex directed dorsally. It is sculptured by numerous small pits and grooves, with these being most strongly developed anteriorly. The relationship of the maxilla to the surrounding bones of the face is similar to that of dicynodonts: it articulates with the jugal, lacrimal, and prefrontal posteriorly; the nasal dorsally; and the premaxilla midway below the external narial opening. The contacts of the maxilla with the prefrontal and nasal are strongly interdigitating sutures. The lacrimal appears to overlay the maxilla, with the suture line being straight in external view. The details of the remaining contacts are uncertain.

Ventrally, the maxilla has a well-developed palatal flange that borders the internal narial opening (Fig. 5). Four sockets are present in the left and five in the right maxilla. These increase in size posteriorly from the first to third, with the fourth being about equal in size to the second in the case of the right maxilla. A distinct canine is not present.

A small portion of the lateral surface of the premaxilla is present ventral to the external narial opening. This has a roughened surface like that of the maxilla. Ventrally, the paired premaxillae have large palatal flanges that form a dicynodontlike secondary palate (Fig. 5). The ventral surfaces of these flanges are roughened by numerous posteriorly projecting spicules of bone. A distinct suture separates the two premaxillae from each other.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A small septomaxilla spans the premaxilla-maxilla suture (Fig. 1). It has no exposure on the lateral surface of the face. The septomaxilla foramen is a small opening located between the septomaxilla and maxilla.

The nasal has a large exposure on the lateral surface of the face and forms the dorsal half of the posterior margin of the external narial opening. The anterior three quarters of the bone has a roughened pitted texture like that of the maxilla. Posterior to this, the lateral surface of the nasal is smooth.

The lacrimal, in lateral view, appears to be a small subcircular bone fitting between the maxilla, jugal, and prefrontal. The orbital edge of the bone has an internally directed flange, although this is incompletely preserved (Fig. 2).

The jugal is reduced to a slender rodlike bone forming the ventral margin of the orbit and articulating with the postfrontal and squamosal posteriorly and with the maxilla and lacrimal anteriorly. No contribution to the formation of the postorbital or zygomatic bar is made by the jugal. Anteriorly, a well-defined groove is present on the lateral surface of the jugal. This may have been associated with the horny beak.

The prefrontal is a triangular bone forming the anterodorsal edge of the orbit. It contacts the lacrimal ventrally, the maxilla and nasal anteriorly, and the frontal dorsally. All of these sutures are squamous interdigitating contacts. The prefrontal is restricted to the lateral surface of the face, the transition from the lateral to dorsal surface occurring at the area of the prefrontal-frontal contact. The lateral surface of the prefrontal is smooth.

The frontals are seen in ventral view. Each frontal contacts the nasal and prefrontal anteriorly, the postfrontal and parietal posteriorly, and its fellow at the midline. No preparietal bone is present,

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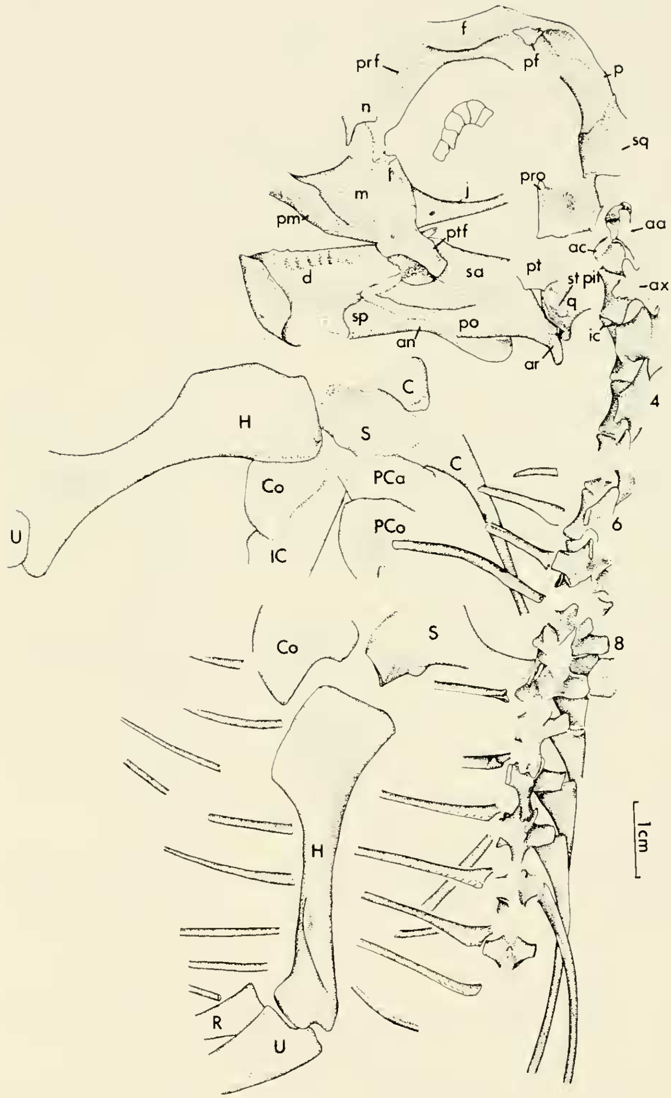
Figure 1. *Galeops whaitsi.* Drawing based on latex peel taken from AMNH-5536.

Abbreviations: an, angular; ar, articular; C, clavicle; Co, coracoid; d, dentary; f, frontal; H, humerus; i, intermedium; IC, interclavicle; j, jugal; l, lacrymal; m, maxilla; n, nasal; p, parietal; pa, prearticular; PCo, procoracoid; pf, postfrontal; pm, premaxilla; po, postorbital; prf, prefrontal; pro, prootic; pt, pterygoid; q, quadrate; qj, quadratojugal; r, radiale; R, radius; S, scapula; sa, surangular; sm, septomaxilla; sq, squamosal; u, ulnare; U, ulna.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so the frontals form the anterior border of the pineal foramen. Laterally, they contribute to the margin of the orbit. Ventrally, strong ridges form the border of the nasal tracts.

The postfrontal is a small, triangular bone wedged between the frontal and postorbital. It has a smooth concave lateral surface.

The postorbital is a tall, narrow bone separating the orbit from the temporal opening. It is supported by the jugal and squamosal ventrally and articulates with the parietal and postfrontal dorsally. It does not extend posteriorly along the parietal to meet the squamosal as is the case in dicynodonts and primitive therapsids generally.

The squamosal is a complex bone that is, in its general structure, like that of dicynodonts. As in dicynodonts, the main body of the bone forms the lateral portion of the occipital plate. The dorsal portion of this area is folded posteriorly so that the posterior rim of the temporal fenestra overhangs the occiput. No such outfolding is seen ventral to the zygomatic bar. A ventrally directed ramus supports the quadrate and quadratojugal and forms the lateral portion of the occipital plate. Laterally, an anteriorly directed zygomatic ramus extends to the jugal. This is a narrow rodlike bone, rather than being flat and beamlike as in dicynodonts. The zygomatic ramus of the squamosal overlaps the jugal, extending well anterior to the posterior edge of the orbit.

The parietals are seen in ventral view (Fig. 4). They have a sutural contact with the frontals and postorbitals anteriorly and with the postparietal posteriorly. Large tabulars are probably present as well, but sutures cannot be clearly identified. Ventrally, each parietal has a crescent-shaped ridge that served as the area of attachment of the epipterygoid and braincase to the skull roof. The

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Figure 2. *Galeops whaitsi.* Drawing based on latex peel taken from counterpart slab of AMNH 5536. Skull and lower jaw bones are shown from medial surfaces.

Abbreviations: aa, atlas arch; ac, atlas centrum; an, angular; ar, articular; ax, axis; C, clavicle; Co, coracoid; d, dentary; f, frontal; H, humerus; ic, intercentrum; IC, interclavicle; j, jugal; l, lacrymal; m, maxilla; n, nasal; p, parietal; PCo, procoracoid; pf, postfrontal; pm, premaxilla; prf, prefrontal; pro, prootic; q, quadrate; R, radius; S, scapula; sp, splenial; sq, squamosal; st pit, stapedial pit; U, ulna.

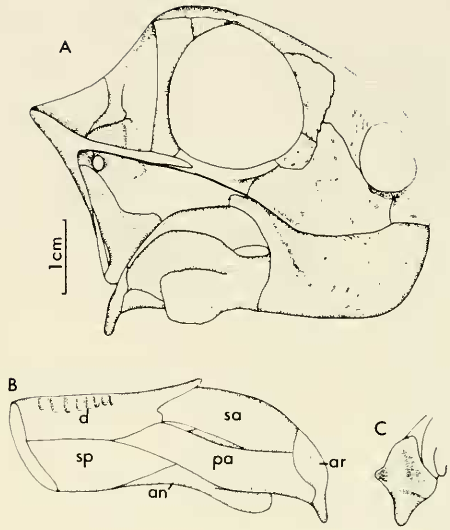

Figure 3. *Galeops whaitsi.* A) reconstruction of skull and lower jaw; B) reconstruction of lower jaw, medial view; C) reconstruction of articular, dorsoposterior view.

Abbreviations: see Figure 2.

parietals extend lateral to this ridge as a ventrally facing shelf that would have provided an area for muscle attachment. This shelf forms a portion of the lateral edge of the temporal fenestra. Anteriorly, a cup-shaped depression is present just anterior and lateral to the area of attachment of the braincase.

The quadratojugal is a small splintlike bone resting on the posterolateral corner of the quadrate ventrally and fitting in a groove on the anterior face of the squamosal dorsally. An oval quadratojugal foramen lies between the quadrate and quadratojugal.

The quadrate is a large bone with a dorsally directed process that fits in a groove in the squamosal, an anteriorly directed flange that

meets the pterygoid, and a ventral expansion that forms the articular surface for the lower jaw. The articular surface is divided into two condyles separated by a deep groove. The lateral condyle is located slightly posterior to the inner condyle. A pit is present on the internal surface of the quadrate that would have received the stapes, although the stapes itself is not preserved.

Braincase: The braincase of *Galeops* is represented by the internal surface of the dorsal half of the occiput (Fig. 4), the lateral surface of the prootic (Fig. 1), and the ventral surface of the basisphenoid (Fig. 5). No sutures can be seen in the occiput. A small posttemporal fenestra is present, surrounded by the squamosal laterally and the occipital plate medially. A groove on the lateral surface of the prootic leads to the temporal fenestra. Two large paired internal carotid foramina are present in the basisphenoid just medial and

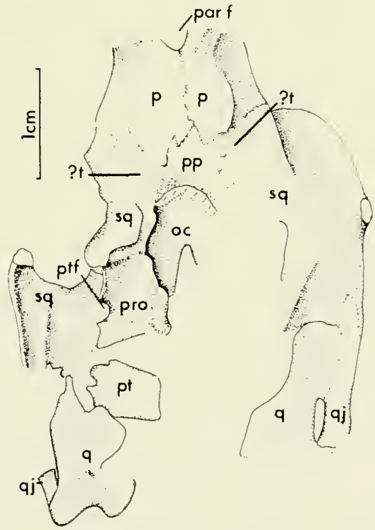

Figure 4. *Galeops whaitsi.* Internal view of posterior surface of skull drawn from latex peel of AMNH 5536.

Abbreviations: oc, occiput; p, parietal; par f, parietal foramen; pp, postparietal; pro, prootic; pt, pterygoid; ptf, posttemporal fenestra; q, quadrate; qj, quadratojugal; sq, squamosal; t, tabular.

posterior to the basipterygoid articulation. Grooves in the basisphenoid lead to these foramina from the posterior edge of the bone. Posterior to the basipterygoid articulation, the lateral edge of the basisphenoid extends ventrally as a large semicircular flange that forms the ventral edge of the fenestra ovalis. This is located well above the level of the stapedial pit on the quadrate, so the stapes would have sloped ventrally, rather than being nearly horizontal as in dicynodonts.

Palate: The palate of *Galeops* (Fig. 5) is primitive in its general structure; a full complement of palatal bones is present, the transverse flange of the pterygoid is present, and the interpterygoidal vacuity is small. An advanced feature is the enlargement of the palatal flanges of the premaxillae to form a secondary palate. The vomers, as in dicynodonts, form vertical plates, although in *Galeops* they are separate ventrally. The palatines have the relationships seen in the primitive anomodont *Otsheria:* each palatine contacts the maxilla and ectopterygoid laterally, the vomers and opposite palatine medially, and the pterygoid posteriorly. The palatines are arched to roof the posterior portion of the internal narial openings. A sharp ridge borders this vaulted area laterally, suggesting that a soft palate was present. The ectopterygoid is a small rectangular bone extending from the transverse flange of the pterygoid to the maxilla. The bone has been displaced slightly, so it is impossible to determine if a lateral palatal foramen was present as in dicynodonts (Cluver, 1975). The pterygoids are partially separated by a small interpterygoid vacuity similar in size and proportions to that of *Otsheria.* The two pterygoids contact one another anterior to this vacuity but do not meet posteriorly, as is the case in dicynodonts, including *Eodicynodon,* the earliest known dicynodont (Barry, 1974). The basipterygoid articulation is unfused. The lateral edge of the transverse flange of the pterygoid is expanded and covered by unfinished bone.

Lower Jaw: The lower jaw of *Galeops* (Figs. 1–3) is short and deep with a vertical unfused symphysis and a straight ventral edge. A fenestra is present on the lateral surface of the jaw between the dentary, surangular, and angular. A distinct coronoid process is not present, although the posterior edge of the dentary extends above

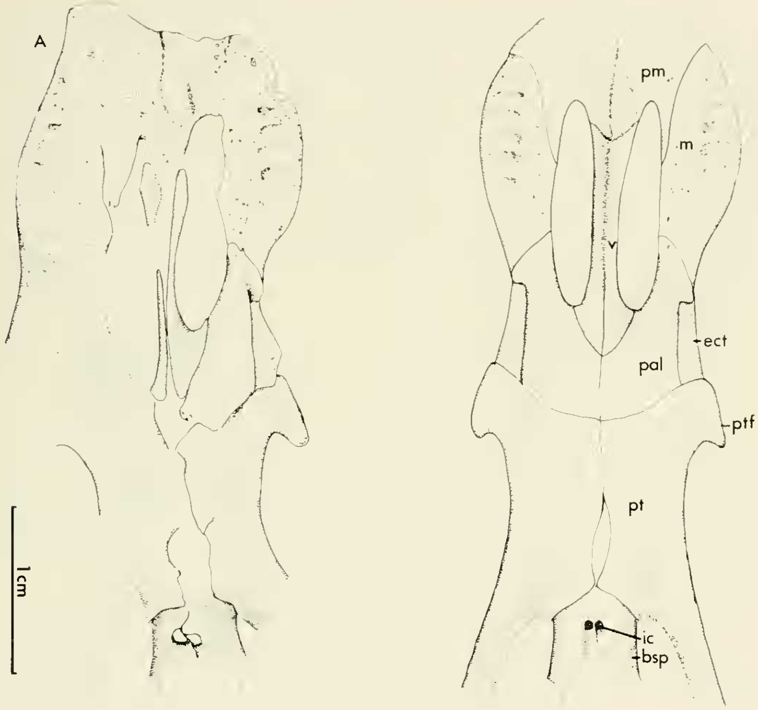

Figure 5. The palate of *Galeops whaitsi*. A) as preserved in AMNH 5536; B) reconstruction.

Abbreviations: bsp, basisphenoid; ect, ectopterygoid; ic, foramen for internal carotid artery; m, maxilla; pal, palatine; pm, premaxilla; pt, pterygoid; ptf, transverse flange of pterygoid; v, vomer.

the level of the postdentary bones. A small ventrally directed retroarticular process is present.

The dentary forms the anterior half of the lower jaw. Except for a small posterior area, the lateral surface of the dentary is covered by numerous small pits and grooves. Posteriorly, the surface is smooth and is depressed below the anterior portion of the bone. This arrangement, which is similar to that of dicynodonts, suggests that the muscles extended onto the posterior portion of the dentary and that a horny beak was present anteriorly. In contrast to most dicynodonts, no longitudinal groove is present on the upper edge of the dentary lateral to the tooth row.

Internally, only the upper half of the dentary is exposed, the ventral half being covered by the splenial. The anterior end of the dentary is without teeth; posterior to this, eight sockets are present for teeth along the lateral margin of the bone. The anterior sockets are slightly larger than the posterior sockets, indicating that tooth size increased anteriorly. There is no indication that a distinct canine was present. All of the sockets are vertical. The tooth row of the dentary is longer than the tooth row of the maxilla, suggesting that some anteroposterior movement of the jaw occurred during closing.

The splenial is restricted to the internal surface of the lower jaw. Posteriorly, the splenial is wedged between the angular and prearticular. It is incompletely preserved anteriorly, although grooves in the dentary show that it extended to the symphysis.

The angular forms most of the lateral surface of the posterior half of the jaw. Its most prominent feature is the reflected lamina, which separates from the angular at the posterior edge of the lateral mandibular fenestra and extends posteriorly and ventrally as a thin sheath of bone.

The prearticular is a broad crescent-shaped bone that extends from the articular to the dentary. It forms the ventral edge of the lower jaw posteriorly, but its lateral exposure is reduced anteriorly so that at the posterior edge of the reflected lamina it is restricted to the internal surface of the jaw. The prearticular most probably formed the margin of the adductor fossa, but since the dorsal portion of the bone is not preserved, the full extent of the fossa is unknown.

The surangular extends from the dentary to the articular, forming the dorsal margin of the postdentary region of the jaw. It is extensively overlapped by the angular so that, in lateral view, it is restricted to the dorsal margin of the jaw, but in medial view, it extends halfway down the internal surface of the jaw.

The articular is supported by the prearticular, angular, and surangular. It forms both the articular surface for the quadrate and the retroarticular process. The articular surface faces strongly posteriorly. It is differentiated into two grooves separated by a rounded ridge. The lateral groove is elongate anteroposteriorly, strongly concave mediolaterally and slightly so anteroposteriorly. A small medially directed shelf forms the medial groove.

The internal surface of the postdentary region is partially covered

by the transverse flange of the pterygoid, so the presence of a coronoid is uncertain.

Vertebrae: The first fourteen vertebrae of *Galeops* are present (Figs. 6, 7), although many of these are incompletely preserved. Cox (1959) differentiated the cervical from the trunk vertebrae of the dicynodont *Kingoria* on the basis of the size of the parapophysis and diapophysis and the thickness of the associated ribs, the cervical vertebrae having more poorly developed parapophyses and more slender ribs. In *Galeops*, a well-developed parapophysis is first seen in the seventh vertebra. No parapophysis can be seen on the corresponding area of the sixth vertebra, although a small one may have been present ventrally. Thus, the first six vertebrae can be considered to be cervicals.

The atlas-axis complex is well-preserved (Fig. 6). It is primitive in its general construction: the atlas centrum and axis are separate, and judging from the articular surfaces, separate atlas and axis intercentra and proatlases would have been present. The atlas arches

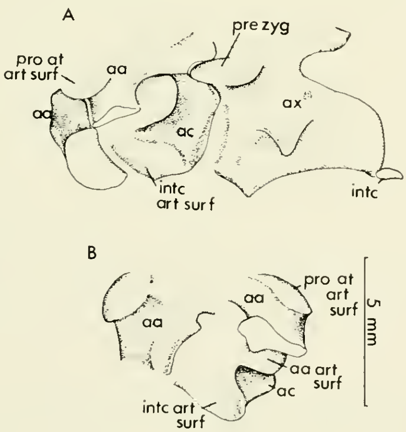

Figure 6. The atlas-axis complex of *Galeops whaitsi*. A) lateral view; B) anterior view of atlas arch and centrum. Drawing based on latex peels from AMNH 5536.

Abbreviations: aa, atlas arch; aa art surf, articular surface for atlas arch; ac, atlas centrum; ax, axis; intc, intercentrum; intc art surf, articular surface for intercentrum; prezyg, prezygopophysis; pro at art surf, articular surface for proatlas.

meet above the neural canal. Transverse processes are present on these elements sloping posteriorly and ventrally. The atlas centrum does not extend to the ventral edge of the vertebral column. It has a trefoil-shaped articular surface anteriorly. The neural spine of the axis is not preserved. The prezygapophysis is convex and faces dorsolaterally. A well-developed transverse process is present on the axis extending posteriorly and ventrally from the base of the neural arch.

Both the cervical and dorsal vertebrae are deeply amphicoelous. A sharp ventral keel is present on the centra. The neural arches are not fused to the centrum, although the sutural attachment is intimate. The base of the neural arch is located anteriorly on the centrum. A large intercentrum is present between the sixth and seventh vertebrae, and presumably intercentra would have been present between the more anterior vertebrae. A small intercentrum is located between the seventh and eighth vertebrae. None is present posterior to this.

A number of structural changes can be seen posteriorly along the vertebral column:

1) The transverse process moves dorsally. The transverse process of the axis is located at the dorsal margin of the centrum. On the fourth vertebra, it is located more dorsally on the lateral surface of the neural arch. The position of the process of the following three vertebrae is similar. A further dorsal migration is seen between the seventh and ninth vertebrae, with the transverse process reaching the level of the zygapophysis.

2) The inclination of the transverse process changes from ventral to dorsal. On the axis, the transverse process slopes ventrally and posteriorly. On the fourth vertebra, the process is nearly horizontal and is directed laterally. On the eighth vertebra, a distinct dorsal inclination is seen. This is further accentuated on the more posterior vertebrae.

3) The parapophyses move dorsally. A distinct parapophysis is first seen on the seventh vertebra, where it is located well down on the anterior edge of the centrum. The intercentrum and posterior edge of the sixth vertebra also contribute to its formation. The parapophysis of the eighth vertebra is located slightly higher, and the articular surface does not extend onto the seventh vertebra. The parapophysis of the eleventh vertebra is located about midway

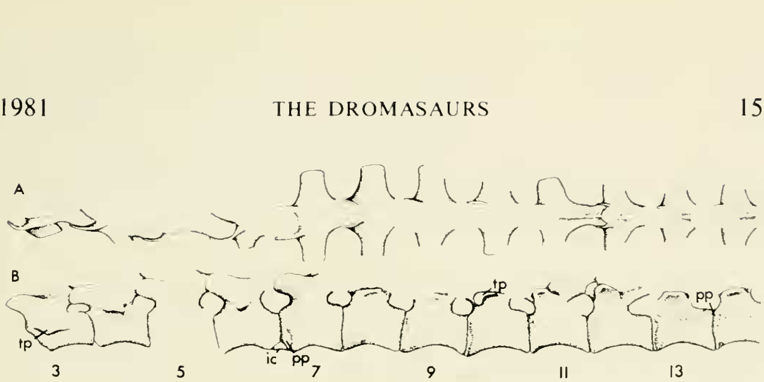

Figure 7. The vertebral column posterior to the axis of *Galeops whaitsi* in A) dorsal and B) lateral views. Based on latex peels taken from AMNH 5536.

Abbreviations: ic, intercentrum; pp, parapophysis; tp, transverse process.

between the dorsal and ventral edges of the centrum. On the fourteenth vertebra, the parapophysis is located on the dorsal margin of the centrum close to the transverse process, although the capitular and tubercular articular surfaces of the rib head remain distinct. There is no indication that the diapophysis migrates ventrally from the transverse process, as in dicynodonts (Cox, 1959).

4) The zygapophyses move closer to the midline. On the sixth vertebra, the first vertebra on which the zygapophyses are clearly preserved, the zygapophyses are located at the edge of the centrum and are inclined about 45° to the horizontal. The seventh to eleventh vertebrae show a medial movement of the zygapophyses and an increase in the angle that they make with the horizontal from about 45° to about 60°. The medial movement of the postzygapophyses results in a coalescence of the processes supporting the articular surfaces, resulting in a single posteriorly directed process.

Ribs: Of the cervical ribs of *Galeops,* only those associated with the fifth and sixth vertebrae are preserved (Figs. 1, 2). Although both of these are incomplete, they are distinctly less robust than the more posterior ribs.

The first nine thoracic ribs are at least partially preserved. All of these are double-headed. The tuberculum terminates the shaft of the rib, and the capitular articular surface is formed by a process that extends ventrally at an angle of about 35° to the shaft. The thoracic ribs are only slightly curved. In the right rib associated with the

twelfth vertebra, the shaft of the rib extends nearly straight from the tubercular surface for about a quarter of the length of the rib. Thus *Galeops* probably had a tall laterally compressed body.

Pectoral Girdle: The pectoral girdle of *Galeops* is formed by the paired clavicles, coracoids, procoracoids, and scapulae and by a single median interclavicle (Figs. 1, 2). There is no evidence that either a cleithrum or an ossified sternum was present.

The scapula has a tall, slender blade and an expanded platelike base. A prominent tubercle for the scapular head of the triceps is present on the posterior edge of the bone just proximal to the glenoid. A distinct acromion process is not present, nor is a scapular spine developed as is the case in dicynodonts (Boonstra, 1966).

The coracoid and procoracoid are subequal in size. The glenoid is formed by the scapula and coracoid. The primitive screw-shaped structure of the glenoid has been lost; the glenoid of *Galeops* is short and faces posterolaterally. The coracoid extends posterior to the glenoid. The coracoid foramen is located within the procoracoid.

The clavicle has a triangular base and a rodlike stem. The interclavicle is a long paddle-shaped element. Its head is not preserved. Distinct grooves for a sternum are not present in the stem.

Humerus: The humerus of *Galeops* is a slender bone with moderately expanded proximal and distal ends in a distinct shaft (Fig. 8). The proximal and distal ends are distinctly, but not strongly, twisted on one another; when viewed proximally, the angle between the long axes of the two ends is about 40°. The proximal end of the humerus curves strongly dorsally; when seen in anterodorsal view (Fig. 8B), the dorsal third of the humerus makes an angle of about 120° with the distal third of the humerus. The entepicondyle is well developed, and an entepicondylar foramen is present. The ectepicondyle is poorly developed, and no ectepicondylar foramen is present. A groove passing proximodistally along the lateral edge of the bone presumably held the nerves and vessels that usually pass through the ectepicondylar foramen. The ulnar articular surface is distinct and well developed. It faces primarily ventrally, although it extends onto the distal end of the humerus. The radial condyle, although distinct, is not a strongly rounded capitulum like that seen in gorgonopsians and dicynodonts (Boonstra, 1965, 1966).

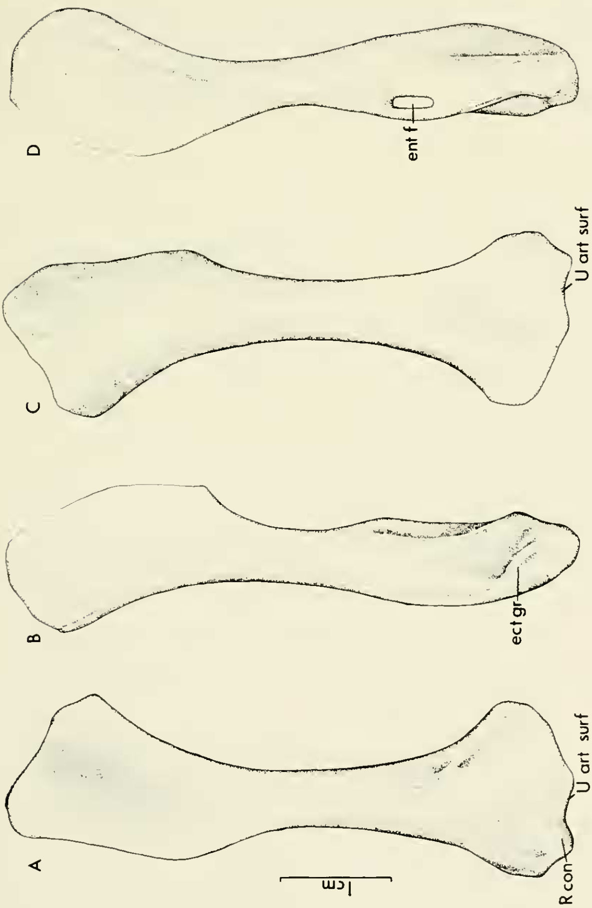

Figure 8. The humerus of *Galeops whaitsi* in A) anteroventral; B) anterodorsal; C) posterodorsal; and D) posteroventral views. Based on AMNH 5536.

Abbreviations: ect gr, ectepicondylar groove; ent f, entepicondylar foramen; R con, radial condyle; U art surf, articular surface for ulna.

Radius: The radius of *Galeops* is a slender bone about 60 percent of the length of the humerus. The proximal articular surface is oval in outline and is slightly concave. The distal articular surface is also oval.

Ulna: The ulna of *Galeops* is slightly longer than the radius (Figs. 1, 2). The olecranon process is prominent, extending well past the humeral articular surface. The humeral articular surface is a well-defined notch. Lateral to this, a distinct articular surface for the radius is present.

Carpus: Only the dorsal surface of the proximal carpal bones of *Galeops* is seen (Fig. 1). The radiale is short and has a small area of finished bone on its dorsal surface. The intermedium and ulnare are elongate. They have a large area of contact with one another proximal to the perforating foramen. A portion of the lateral centrale is present. This supports the intermedium and forms the distolateral corner of the perforating foramen.

GALEPUS

Materials and Methods: Galepus is represented by a single species, *Galepus jouberti*, and by a single specimen, AMNH 5541, that comes from the *Cistecephalus* zone of the Beaufort series of South Africa. Much of the skull and skeleton is represented by impressions in a coarse sandstone from which latex peels were made. Unfortunately, the counterpart block was not preserved, so it was not possible to cast individual elements in three dimensions.

Skull: The skull of *Galepus* is represented by a cast of the internal surface of the roofing bones and of the palatal flanges of the premaxillae (Figs. 9, 12). It is similar to that of *Galeops* in its general structure: the orbits and external narial openings are large; the face and postorbital region of the skull are short; a large oval pineal opening is present; the ventral margin of the postorbital region of the skull is deeply emarginated; the occiput slopes forwards; the orbit is bounded posteriorly by a tall narrow postorbital; a secondary palate formed by the palatal flanges of the premaxillae is present; and the internal surface of the parietal is marked by a crescentic ridge and a cup-shaped depression antero-

Figure 9. *Galepus jouberti.* Drawing based on latex peel taken from AMNH 5541. Skull and lower jaw bones viewed from medial surface.

Abbreviations: C, clavicle; cal, calcaneum; cen, centrale; Co, coracoid; ect for, ectepicondylar foramen; F, femur; H, humerus; IC, interclavicle; IL, ilium; IS, ischium; mc 1, first metacarpal; mt 5, fifth metatarsal; PCo, procoracoid; PU, pubis; r, radiale; R, radius; U, ulna.

lateral to this ridge. Unfortunately the sutures referred to by Broom (1914) have been obliterated, so the exact relationships of the individual skull elements are uncertain.

The left lower jaw is visible in internal view. It is more slender than the jaw of *Galeops*, and its outline differs: the ventral margin of the jaw, rather than being straight as in *Galeops*, is slightly concave in profile, and the dorsal margin of the postdentary region extends nearly straight from the dentary to the articular, rather than being gently convex as in *Galeops*. A splenial is not preserved, but grooves in the dentary indicate that it extended to the symphysis. The sutures between the postdentary bones cannot be identified.

Six small peglike teeth are preserved in the dentary and an empty aveolus is present anterior to these. A small edentulous region is present anterior to the tooth row. Unlike *Galeops* where the sockets, and presumably the teeth they contained, are vertical, the teeth of *Galepus* slope anteriorly.

Postcranial Skeleton: A series of eighteen dorsal vertebrae of *Galepus* is present. These are deeply amphicoelous and show a sutural attachment between the neural arch and centrum. The structure of the neural arch is seen clearly only in the fifth vertebra from the anterior end of the preserved series. It is like the neural arch of the corresponding vertebra in *Galeops:* the zygapophyses are strongly tilted and are near the midline, the postzygapophyses are coalesced so the articular surfaces appear to be formed by a single posteriorly directed process, and the transverse processes are large dorsolaterally directed structures located at the level of the zygapophyses.

The caudal region is represented by two disconnected series of vertebrae, an anterior series of nine vertebrae and a posterior series of eight vertebrae. They are separated by a space that would have been occupied by six vertebrae and are separated from the sacral region by a space that would have been occupied by about eight vertebrae. Thus the tail would have included at least 31 vertebrae. These decrease in both height and length posteriorly. The zygapophyses slope less steeply than in the dorsal series. A prominent transverse process is located at the base of the neural arch on the first vertebra in the series. No transverse process is seen on any of the more posterior vertebrae. Haemal spines and arches are present

between all the vertebrae in the proximal series and between the first two vertebrae in the posterior series.

Eighteen ribs are at least partially preserved on the right and six on the left side. In all the ribs, the curvature is greatest near the head, with the distal half of the rib being nearly straight and at an angle of 30° to the proximal portion. The heads of the first three ribs on the left side and the last two ribs on the right side are visible. The anterior ribs are double-headed. The posterior ribs are single-headed.

The pectoral girdle is seen in internal view. A large interclavicle is present with a paddle-shaped stem and a diamond-shaped head. No ossified sternum is present. The clavicle has a long narrow riblike stem and a triangular head. The coracoids, procoracoids, and scapulae are too poorly preserved for their structure to be fully determined.

The humerus of *Galepus* is like that of *Galeops* in its proportions and general features. In both, the entepicondyle is well developed, the ectepicondyle is reduced, the proximal and distal ends are distinctly twisted on one another, the ulnar surface faces strongly ventral but also extends onto the distal surface of the bone, and the pectoral crest is restricted to the proximal third of the bone. The humerus of *Galepus* differs from that of *Galeops* in having an ectepicondylar foramen and in the lack of an upturning of the proximal end, the dorsal edge being nearly straight in anterodorsal view.

Only the medial surface of the proximal end of the ulna is preserved. As in *Galeops* an olecranon process is present, and the medial surface of the proximal end of the ulna is concave. The right radius is seen in lateral aspect. It is like the radius of *Galeops* in its proportions and in having a slight S-shaped curve.

The hand overlies the foot, although much of the hand is missing, exposing the metatarsals and phalanges of the foot.

Only three elements of the carpus are present, these being the radiale, lateral centrale and first distal carpal. The radiale is short and without finished bone. The first distal carpal is subcircular and has a large area of finished bone on its ventral surface.

Of the metacarpus, only the first metacarpal is present. This is a short phalangelike element. A large tubercle is present on the lateral edge of the bone near its proximal end. The toes are represented by three long, clawlike terminal phalanges.

The pelvis is seen in internal view. It is primitive in having a large pubis and ischium and in having well-developed anterior and posterior extensions of the iliac blade. An advanced feature is the enlargement of the obturator foramen.

The dorsal surface of the proximal end of the left femur is visible. The proximal end of the femur is tilted dorsally about 35° from the shaft of the bone.

The tarsus is represented by an incompletely preserved right calcaneum, centrale, and the first four distal tarsals, all visible in ventral view. The calcaneum is a tall, platelike element with a notch for the perforating foramen on its medial edge. The centrale is a cubical cartilage-covered element. The first three distal tarsals are subequal in size. The fourth is larger, although it is less than twice the size of the third in its linear dimensions.

All five metatarsals are present, visible in ventral view. They increase in size from the first to the fourth with the fifth being about equal to the third in length. The phalangeal formula of the pes is 2,3,?,?,3. The terminal phalanges, where known, are elongate, clawlike elements.

GALECHIRUS

Materials and Methods: Galechirus is represented by a single species, *Galechirus scholtzi,* and by two specimens: SAM 1068, which shows the front half of the skull and the lower jaw in lateral view and much of the postcranial skeleton (Fig. 10); and AMNH 5516 (now housed in the South African Museum), which shows a pelvic and pectoral limb and fragmentary ribs and vertebrae (Fig. 11). Both of these specimens come from the *Cistecephalus* zone of the Beaufort series of South Africa (Kitching, 1977). They are preserved as natural casts. Molds taken from these specimens provided a positive image that served as the basis for the descriptions and drawings.

Skull: The skull of *Galechirus* (Fig. 10) is like that of *Galeops* in having large orbits and external narial openings, a short temporal region, and a deep emargination of the cheek posterior to the orbit. In contrast to the condition in *Galeops, Galechirus* retains premaxillary teeth and has a more elongate face.

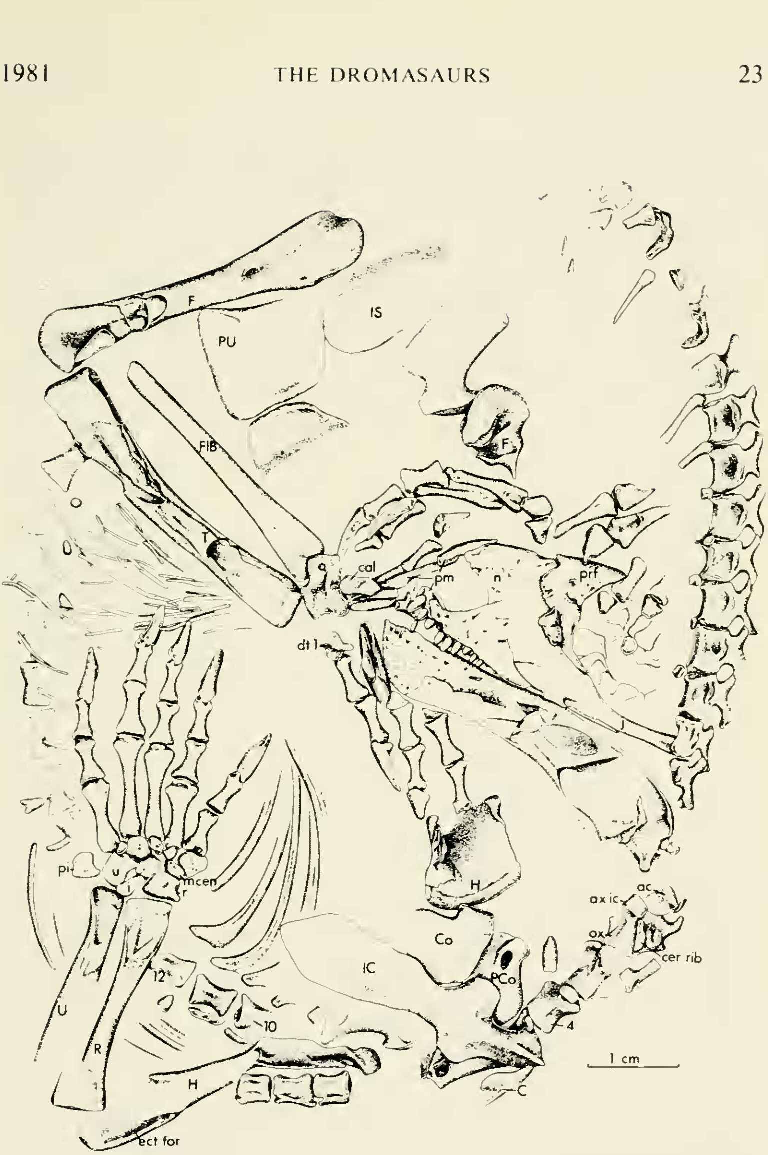

Figure 10. *Galechirus scholtzi.* Drawing based on latex peel taken from SAM 1068.

Abbreviations: a, astragalus; ac, atlas centrum; ax, axis; ax ic, axis intercentrum; C, clavicle; cal, calcaneum; cer rib, cervicle rib; dt 1, first distal tarsal; ect for, ectepicondylar foramen; F, femur; FIB, fibula; H, humerus, i, intermedium; IS ischium; j, jugal; m cen, medial centrale; pi, pisiform; pm, premaxilla; prf, prefrontal; PU, pubis; T, tibia; u, ulnare; U, ulna.

The arrangement of the bones of the face in *Galechirus* is similar to that of *Galeops.* The premaxilla-maxilla contact is located midway below the external narial opening. A separate bone, presumably the septomaxilla, is present internal to the premaxilla-maxilla contact. The maxilla meets the nasals midway along the posterior edge of the external narial opening. The maxilla-nasal suture slopes dorsoposteriorly from this point. Unfortunately, the sutures between the maxilla and more posterior bones are obscure, so the relationship of these bones is uncertain. Six small peglike teeth are present in the maxilla, and an empty socket is present posterior to these. The anterior three teeth are subequal in size and are slightly larger than the posterior three teeth.

The premaxillae are separate. Each premaxilla has a well-developed dorsal ramus that extends between the nasals and a ventral ramus that meets the maxilla midway below the external narial opening. The right premaxilla, which is seen in internal view, contains two large, procumbent, chisel-shaped teeth. Three teeth are present in the preserved portion of the left premaxilla. The posterior two are approximately equal to the maxillary teeth in size and are vertically oriented. The more anterior tooth is slightly larger and slopes anteriorly. The missing portion of the premaxilla probably held two large procumbent teeth similar to those seen in the right premaxilla.

The prefrontal, which has been displaced slightly, is a triangular element forming the anterodorsal margin of the orbit. Its lateral surface is smooth and curves onto the dorsal surface of the skull.

The suborbital portion of the jugal is a narrow rodlike bone. Posteriorly, a groove is present on its lateral surface, probably for an overlying zygomatic branch of the squamosal.

Lower Jaw: The lower jaw of *Galechirus* is long and slender. Its ventral edge curves upwards, and the symphysis slopes forward. The dentary forms the anterior two-thirds of the jaw. Its lateral surface is covered by numerous small pits and grooves anteriorly. Posteriorly, the surface is smooth and is recessed below the more anterior portion of the dentary. Presumably the adductor muscles inserted on this area of the dentary. Only one tooth is preserved in the dentary. This is a small peglike element located well anteriorly. There does not appear to be room anterior to this for large

procumbent teeth similar to those seen in the premaxilla, nor is there any evidence that such teeth were present.

The dorsal edge of the postdentary region of the jaw curves evenly from the posterior edge of the dentary to the articular. A fenestra is present between the dentary and the postdentary bones. The reflected lamina of the angular separates from the angular at the posterior edge of the fenestra. A small ventrally directed retroarticular process is present beneath the jaw joint. The sutures between the individual bones of the postdentary region of the jaw are not visible.

Postcranial Skeleton: The vertebral column of *Galechirus* is partially preserved in SAM 1068. Anteriorly, four cervical vertebrae are present between the posterior end of the jaw and the pectoral girdle. The first vertebra in this series is the atlas, the centrum of which is seen in lateral view. As in *Galeops*, it does not reach the ventral surface of the vertebral column. A large axis intercentrum is present as a distinct element between the atlas centrum and the axis. The following vertebrae are short and broad, their length being about equal to their width across the posterior end of the centrum. The axis has a posteroventrally directed transverse process located well down on the neural arch. The centrum does not have a sharp ventral keel, although a low ridge is present. The following two vertebrae are seen in ventral view. A distinct ventral keel is present, and intercentra are present between each of these vertebrae.

A series of three dorsal vertebrae, probably the tenth to twelfth, lies between the shoulder girdle and the hand. These are seen in ventral view. The keel has been reduced and intercentra are absent. Distinct articular surfaces for the heads of the ribs are not visible.

Faint traces of eight presacral vertebrae are present between the wrist and the knee. Little of their structure can be determined.

The caudal vertebrae are represented by two series: an anterior series of twelve vertebrae and a more posterior series of three vertebrae. A space equal in length to four centra is present between the anterior series and the pelvis, and the two sections of the tail are separated by a space equal in length to about ten centra. Thus, the tail would have had in excess of 29 vertebrae.

The caudal vertebrae decrease both in height and length posteriorly. Haemal arches are present between each of the first ten vertebrae, and transverse processes are present on each of the

vertebrae in the anterior series. The more posterior vertebrae have neither transverse processes nor haemal arches.

Three ribs are preserved in SAM 1068. These are associated with the three vertebrae seen between the shoulder girdle and the hand. The more anterior of these is clearly double-headed. The separation of the two articular surfaces is less distinct posteriorly.

Small, needle-like gastralia are present posteriorly, but these are disturbed so their natural arrangement is unknown. This is the only evidence of gastralia in therapsids (Romer, 1956).

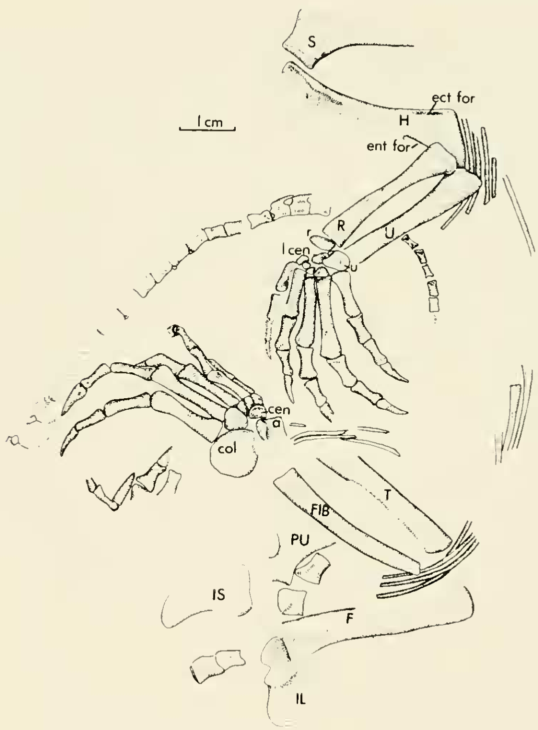

Figure 11. *Galechirus scholtzi.* Drawing based on cast of AMNH 5516 (now housed in the South African Museum).

Abbreviations: a, astragalus; cal, calcaneum; cen, centrale; ect for, ectepicondylar foramen; ent for, entepicondylar foramen; F, femur; FIB, fibula; IL, ilium; IS, ischium; l cen, lateral centrale; PU, pubis; r, radiale; R, radius; S, scapula; T, tibia; u, ulnare; U, ulna.

The pectoral girdle is seen in ventral view in SAM 1068 and in lateral view in AMNH 5516. The scapulae have tall, slender blades and expanded platelike bases. A distinct rugosity on the posterior edge of the scapular blade just proximal to the glenoid marks the site of the origin of the scapular head of the triceps. An acromion process is not present.

The coracoid and procoracoid are both large, with the coracoid extending well posterior to the glenoid. The procoracoid foramen is located within the procoracoid just proximal to the glenoid. The interclavicle has a diamond-shaped head and a broad paddle-shaped stem. The head of the interclavicle is recessed ventrally to receive the medial end of the clavicle.

The left humerus is seen in ventral view in both specimens. The proportions of this element are similar to the proportions of the humerus of *Galeops:* it is a slender bone with a well-defined shaft and with little expansion of the proximal and distal ends. The pectoral crest is restricted to the proximal third of the bone. In contrast to the condition in *Galeops,* both an ectepicondylar and ectepicondylar foramen are present.

The radius is a slender bone, slightly shorter than the humerus. It has a slight S-shaped curvature. The ulna is almost identical to that of *Galeops* in its proportions and in the development of the articular surfaces, although the olecranon process is less well developed. This difference may be a result of differences in the ontogenetic stage of development of the specimens.

A complete carpus is present in SAM 1068 and most of the carpus is present in AMNH 5516. All the elements primitively present in the synapsid carpus are present, although these are all shortened proximodistally so the length of the carpus is less than that of the metacarpus. A distinctive feature is the expansion of the ulnare to form a flat platelike bone.

The metacarpals increase in length from the first to the fourth, with the fifth being about equal to the second in length. The phalangeal formula is 2,3,3,3,3. The terminal phalanges are elongate, laterally compressed, clawlike elements.

The pelvis is seen in ventral view in SAM 1068 and in lateral view in AMNH 5516. The pubis and ischium are large, platelike elements. The pubis is damaged, so the size of the obturator foramen is uncertain. The ilium is not completely known, although the pre-

served portion shows that it had a tall, slender blade that extends posterior to the acetabulum.

The femur is seen in postaxial view in both specimens. It is equal in length to the humerus. The head of the femur is incompletely preserved, although there is no indication of a dorsal tilting of the proximal end such as is seen in *Galepus*. Also, no downturning of the distal end of the femur is seen.

The tibia and fibula are elongate, slender bones approximately equal in length to the femur and substantially longer than the radius and ulna. Both bones are slightly curved with the concave edges of the bones facing one another. The tibia is more robust than the fibula, the diameter of the tibia at its narrowest point being about twice the minimum diameter of the fibula.

A nearly complete tarsus is seen in dorsal view in AMNH 5516, and an astragalus is seen in dorsal view in SAM 1068. The calcaneum is a large platelike bone. The astragalus is L-shaped. A perforating foramen passes between the astragalus and calcaneum. Distal to the perforating foramen, the articular surface on the astragalus for the calcaneum is strongly convex and extends onto the dorsal surface of the bone. Proximal to the perforating foramen, the articular surface on the astragalus for the calcaneum is concave. The tibial articular surface is restricted to the medial edge of the astragalus. The centrale is a small, cartilage-covered bone located between the astragalus and first four distal tarsals. The distal tarsal row consists of four elements, the fifth distal tarsal having been lost. The first three are subequal in size, the fourth is about three times the size of the third in its linear dimensions.

The metatarsals increase in length from the first to the fourth, with the fifth being about equal to the third in length. The phalangeal formula is 2,3,3,3,3. The terminal phalanges are elongate, laterally compressed clawlike elements.

DISCUSSION

In considering the general evolution of therapsids, Hopson (1969) recognized three basic groups: the Dinocephalia, characterized by an interlocking of the incisors and the presence of a jaw joint that permits no anteroposterior movement of the jaw; the Theriodontia, characterized by the development of a movable quadrate permitting some anteroposterior movement of the lower jaw; and the Anomo-

dontia, characterized by the ventral emargination of the cheek posterior to the orbit and a jaw joint that permits considerable anteroposterior movement of the lower jaw on the fixed quadrate. The emargination of the cheek in the dromasaurs immediately indicates that they belong within the Anomodontia. This placement is supported by features of the skull of dromasaurs that are similar to other anomodonts, including: 1) the formation of a secondary palate by palatal flanges of the premaxillae and 2) the presence of a lateral mandibular fenestra.

The most primitive anomodonts known are the venjukoviamorphs *Otsheria* and *Venjukovia* from the Middle Permian of Russia. These show the diagnostic feature of an emarginated cheek, but, relative to dicynodonts, retain a primitive jaw joint, a primitive palate, and primitive features in the temporal region (Watson, 1948; Olson, 1962; Barghusen, 1976). In many respects, the dromasaurs are at the same grade of evolution as are the venjukoviamorphs. This is demonstrated by the following features, which are shared by dromasaurs and the venjukoviamorphs and which are different from the more derived condition seen in dicynodonts:

1) No outfolding of the squamosal is present ventral to the zygomatic ramus of the squamosal. In dicynodonts, such an outfolding is present.
2) The palate is more primitive in showing a small interpterygoid vacuity, transverse flanges on the pterygoids, an unfused basipterygoid joint, and a smaller secondary palate. In dicynodonts, the interpterygoid vacuity has enlarged so that it extends forward between the posterior ends of the vomers, the transverse flanges of the pterygoids have been lost, and the pterygoids are sutured to one another posterior to the interpterygoid vacuity (Cluver, 1970).
3) The articular, as in *Venjukovia* (Watson, 1948), retains a central ridge with two concave depressions on either side of it. In dicynodonts, the central ridge is convex in profile, and a concave area is present anterior to this (Crompton and Hotton, 1967).

In addition, a number of features seen in the dromasaurs, but not known at present in the venjukoviamorphs, are more primitive than the condition in dicynodonts. These include:

1) A separate atlas centrum and axis intercentrum are present in the dromasaurs. In dicynodonts, these fuse to the axis (Cox, 1959). However, the atlas centrum and axis may fuse during ontogenetic development in the dromasaurs.
2) No scapular spine or acromion process is present on the scapulocoracoid. In dicynodonts, both these features are present (Boonstra, 1966).
3) The shape of the interclavicle and the absence of a sternum in the dromasaurs is primitive. In dicynodonts, the interclavicle is short and a large sternum is present (Boonstra, 1966).
4) The iliac blade in the dromasaurs is primitive in having a well-developed posterior process. In dicynodonts, the anterior ramus of the ilium is more strongly developed than the posterior ramus (Boonstra, 1966).

Despite the primitive structure of the dromasaurs, features are present that are advanced over the condition seen in the venjukoviamorphs and are similar to the condition seen in dicynodonts. One of these is the structure of the jugal. In *Otsheria,* the jugal is a triradiate bone retaining well-developed zygomatic and postorbital branches. In *Venjukovia,* the postorbital branch has been reduced although it is still present (Barghusen, 1976). In both dromasaurs and dicynodonts, the postorbital and zygomatic branches of the jugal have been reduced or lost. A second advanced feature is the presence of a smooth area on the posterior end of the dentary that suggests that the adductor muscles extended onto the lateral surface of the dentary. In *Venjukovia,* an external mandibular muscle was present, although it had only a small area of insertion on the lateral surface of the dentary (Barghusen, 1976). A third advanced feature is the structure of the septomaxilla. In *Otsheria* and *Venjukovia,* as in primitive therapsids generally, the septomaxilla is a large element with an exposure on the lateral surface of the face. In dicynodonts and dromasaurs, the septomaxilla is reduced; in the dromasaurs, it is restricted to the floor of the external narial opening.

This combination of primitive and derived features demonstrates that the dromasaurs are members of a grade of evolution intermediate between the venjukoviamorphs and the dicynodonts, but it does not demonstrate that it is a monophyletic group. For this, it is necessary to show that features are present in the three genera that are advanced over the primitive anomodont condition but are not

shared with dicynodonts. The most obvious such feature is the dentition, which consists of reduced peglike teeth. This is a clear difference from both the primitive anomodont condition and the dicynodont condition in which distinct canines are present. An additional derived feature that separates dromasaurs from dicynodonts is the presence of a tall, narrow postorbital and a slender, rodlike lower temporal bar. In dicynodonts, the postorbital bar is low and the lower temporal bar is a flat, beamlike element.

Also the absence of a contact between the postorbital and squamosal is a derived feature different from the condition in both dicynodonts and venjukoviamorphs, where the postorbital extends along the upper margin of the temporal opening to reach the squamosal. However, the only dromasaur in which the posterior extent of the postorbital is known is *Galeops*, so the possibility that this is a derived feature present only in that genus cannot be discounted.

Thus the present evidence, although not conclusive, suggests that the dromasaurs are a natural group. Within the group, the three genera can be placed in a single structural sequence with *Galechirus* being the most primitive and *Galeops* being the most derived member of the sequence. The features that document this series are:

1) *The Tooth Row:* In *Galechirus*, premaxillary teeth are present; in *Galepus*, premaxillary teeth are absent but the edentulous region is short; in *Galeops*, a large edentulous region is present.
2) *The Proportions of the Face:* In *Galechirus*, the face is relatively long; *Galepus* and *Galeops* show a progressive reduction in the length of the face (Fig. 12).
3) *The Lower Jaw:* In *Galechirus*, the lower jaw is slender and the ventral border is concave; in *Galepus* and *Galeops*, a progressive decrease in the length of the jaw is seen and the ventral margin becomes straight (Fig. 12).
4) *Humerus:* In *Galechirus* and *Galepus*, the dorsal margin of the humerus is straight when seen in anterodorsal view. In *Galeops*, the proximal end of the humerus curves strongly dorsally.
5) *Ectepicondylar Foramen:* In *Galechirus*, a well-developed ectepicondylar foramen is present; in *Galepus*, this foramen is reduced; in *Galeops*, an ectepicondylar foramen is absent.

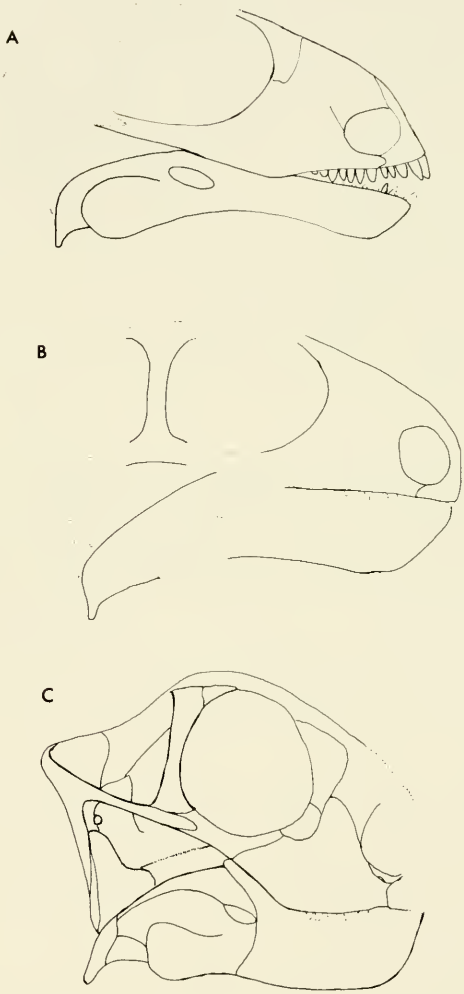

Figure 12. Reconstructions of the skulls of the dromasaurs. A) *Galechirus sholtzi;* B) *Galepus jouberti;* C) *Galeops whaitsi.* Not drawn to scale.

Since the most derived member of this sequence is the earliest, these three genera cannot represent successive stages in a single evolving lineage. Rather, they must be regarded as members of distinct grades of evolution in a single monopholetic radiation.

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